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Effects of handedness on the skull and shoulder bones

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EFFECTS OF HANDEDNESS ON THE SKULL AND SHOULDER BONES

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Abstract

The unique configuration of the human clavicle and mastoid process suggests a functional connection between the head and shoulders in humans. The hypothesis in this study is that the clavicle, scapula and head form a functional complex and are interconnected by the sternocleidomastoid and trapezius muscles. In this complex, the trapezius muscles attach to the skull and become active when loads are carried. The sternocleidomastoid muscles are anchored to the clavicles; when loads are being carried, they act as guy ropes for the head, thereby keeping the head from being extended by the force of the contracting trapezius muscles. These muscle actions can be expected to leave evidence on the bones to which they attach, and this evidence could be measurable. The hypothesis was tested by comparing the mensural and morphological bilateral asymmetries of 15 skeletal features, most of which would likely be affected by the functioning of this complex in individuals. The hypothesis is supported by the results which show that four character pairs of the functional complex (i.e., rise of the superior nuchal line, width of the mastoid, breadth of the scapula, diameter of the humerus) display significant directional asymmetry in right-handed individuals; the sample size of left-handed individuals was too small to provide meaningful results.

1. Introduction

The mastoid process is much larger, relative to body size, in humans than in most other primates and mammals (Krantz, 1963). The clavicle is also well-developed in humans (Trotter, 1885). Despite a number of studies on these subjects, the causes for these morphological distinctions of humans have not been resolved. This research focuses on these morphologies as they are affected by mechanical loading.

The robust mastoid process is a characteristic feature of the human skull (Krantz, 1963). At birth, it is not yet formed, but becomes noticeable after a year or two (Leidy, 1883; Romanes, 1964). After a year, an infant is sitting upright, crawling or walking, holding up her own head, and using her hands in different activities. Hence, the mastoid process appears to be related to its function as the attachment site of the sternocleidomastoid muscle, because the mastoid process provides a mechanical advantage to the muscle. According to Krantz (1963), the simultaneous bilateral contraction of the sternocleidomastoid muscle returns the head that has been pulled backwards to a horizontal position. If the sternocleidomastoid muscle attached directly to the skull surface, the contraction of the muscle would pull the neck forward, but the head would be pulled farther back. The presence of the mastoid process, however, enables the sternocleidomastoid muscle to attach anterior to the axis of the atlanto-occipital joint, thereby allowing the head and neck to be pulled forward. In a later article, Krantz (1980) considered the mastoid to be a part of a trait complex that evolved in connection with the evolution of spoken language. He also suggested that the anterior placement of the mastoid process on the skull is a result of the elongation of the pharynx and the skull's subsequent adaptations to match this elongation. Neither of these studies of the mastoid process addresses its large size in humans.

The characteristically thick clavicle in humans acquires its s-shape *in utero* (Gardner, 1968; Black and Scheuer, 1996). According to White (2000), the clavicle acts as a bony strut that keeps the shoulders from collapsing. Inman and Saunders (1946) support the idea that the clavicle is important by suggesting that there is less stability in the loaded arm in extreme ranges of motion when an individual is without a clavicle or with a damaged one. Other authors, however, disagree about the importance of the clavicle's function. Basmajian (1963) writes that the clavicle is no more than an artificial boundary between muscles. Abbott and Lucas (1954) suggest that this boundary is not necessary; by stitching together the muscles that attach to the clavicle, the function of the shoulder would be basically unaffected. Black and Scheuer (1996) support the previous authors by reporting that the clavicle, other than serving as an attachment site for muscles, is simply superfluous.

Although the functions of the mastoid process and clavicle may be argued, they are connected by the sternocleidomastoid muscle and are integral parts of a structural complex, which includes the skull and the scapula and is named the cranio-cervico-omo-clavicular complex in this study. In addition, the trapezius muscle is part of this complex, because it acts with the sternocleidomastoid muscle during movements of the head and neck (Simons *et al.*, 1999; Moore and Dalley, 2006), and attaches in part to the superior nuchal line of the skull and to the spine of the scapula. The anterior scalene muscle is also discussed as part of this complex because it helps move and stabilize the neck and head while the arms and shoulders are moving.

Interestingly, the distinctive mastoid process and clavicle are great liabilities for humans under certain conditions. For example, mastoiditis, an infection and inflammation of the air cells of the mastoid process, which are connected with the middle ear cavity, can damage the middle ear and facial nerve and even be life-threatening if left untreated (Moore and Dalley, 2006). The clavicle, in turn, can also be a liability. Shoulder dystocia occurs when the wide shoulders, which are held apart by the clavicles, have difficulty passing through the birth canal (Al Hadi *et al.*, 2001). To get the shoulders through the birth canal, one arm of the baby often must be pulled out ahead of the other. During this procedure, the nerves and blood vessels of the arm easily can be compressed between the clavicle and the first rib (Moore and Dalley, 2006) and paresis or spasticity of the arm muscles (Erb's Palsy) may result (Pugh, 2000; Al Hadi *et al*., 2001). Considering that the mastoid process and clavicle in their present states can be serious liabilities, they must have a crucial function or they would have been eliminated or modified by natural selection in early humans.

As a working hypothesis for this study, the mastoid process and clavicle in humans are surmised to be related to the development and evolution of erect posture and bipedality, in the course of which the shoulder girdle became essentially suspended from the skull. As a result, when a load is lifted or carried, the shoulder girdle tends to be pulled down by the weight and has to be held in place and stabilized by the counteracting muscle force of the upper portion of the trapezius muscle. Because of its orientation, the trapezius muscle also exerts a medial force, which, in turn, is counteracted by the clavicle to prevent the shoulder from being pulled medially. The contraction of the trapezius muscle not only pulls the shoulder upwards, it also pulls the head backwards. The sternocleidomastoid muscle, attaching on the clavicle and mastoid process, counteracts this force and keeps the head from being pulled back as a result of shoulder stabilization during the lifting or holding of weights.

To test the validity of this hypothesis as an explanation for the large mastoid process and thick clavicle in humans, a natural experiment was designed that involves human handedness. The frequent, and often strenuous, preferential use of one arm over the other has visible effects on the involved skeletal elements (Trinkaus *et al.*, 1994; Kannus *et al.*, 1995; Steele and Mays, 2005; Ruff *et al.*, 2006). Hence, the lifting and carrying of loads and the related actions of the sternocleidomastoid and trapezius muscles should leave evidence of this activity on the bones to which they attach. Because humans lift and carry objects frequently on a favored side, this preferential use can be expected to affect the involved bones unequally on each side. This prediction can be tested by comparing the sizes of characters on the preferred side with those on the other side. In doing this, the effects of the use of the arms and shoulders can be tested in the same individual.

The expected results of this natural experiment are qualitative and quantitative bilateral asymmetries, of which there are three types: fluctuating asymmetry, antisymmetry, and directional asymmetry. Fluctuating asymmetry describes the natural, random morphological asymmetry that is assumed to be caused by the random processes of development as opposed to being caused by function, such as the preferential use of one side (Van Valen, 1962). Bilateral asymmetry caused by function (e.g. handedness) is known as either antisymmetry or directional asymmetry (Van Valen, 1962). Antisymmetry is random morphological asymmetry that would be found in populations (e.g. adult rhesus monkeys and some chimpanzees) where about 50% of the population shows a preference for one hand and the other 50% shows a preference for the opposite hand (Warren, 1953; Van Valen, 1962; McGrew and Marchant, 1992). Directional asymmetry is non-random morphological asymmetry that would be found in populations (e.g. humans) where the majority of the population shows a preference for the same hand and arm over the other (Van Valen, 1962; Coren and Porac, 1977; Holder, 2008).

The asymmetries from this sample will be analyzed to see if they could be evidence of the preferential use of one hand and arm. If there is skeletal evidence of preferential hand use, then there is some evidence that the cranio-cervico-omo-clavicular complex is a functional complex. Then, further research into this complex can be undertaken.

2. Materials and Methods

2.1. Materials

Features on 101 modern human skeletons from the William M. Bass collection at the University of Tennessee, Knoxville, were measured. Only males were used, because their muscle attachment sites tend to be more pronounced than those of females and, therefore, easier to measure. The sample included 93 white males, 6 black males, and 2 Hispanic males. These individuals lived during the 20^{th} century and were donated to the collection between the years of 2000 to 2005. The majority of individuals (i.e., 86) were between the ages of 40 and 79, at the time of death. Only individuals with intact skulls were included in the study. Because the skull was always measured first (see below), some other missing or damaged skeletal elements were discovered later and certain features could not be measured. Aside from the Bass skeletal collection, several individual bones from the Louisiana State University Physical Anthropology Cadaver collection were used in ascertaining the measurement error.

2.2. Methods

2.2.1 Quantitative Characters

Measurements were taken in two rounds, with the first round comprising the skull and the second round comprising the other bones (i.e., clavicle, scapula, humerus, first rib, mandible and femur). Measurement tools included a flexile tape measure, an osteometric board, and sliding calipers. All measurements were taken once and reported to the nearest one tenth of a millimeter. Unconventional measurements, such as the circumference of the mastoid process, were measured with a piece of moist twine. The twine was marked with a pencil at the point where its wrapped ends met, thereby marking two points on the twine. The twine was then straightened and measured from pencil mark to pencil mark with sliding calipers. For this measurement and the thickness of the scalene tubercle of the first rib, the average of three measurements was recorded.

2.2.2. Selection of Measurements

The mastoid process was observed as being obviously different when the left and right sides were compared (M. L. Osborn, unpublished data). Length is the only standard measurement for the mastoid process (Moore-Jansen *et al*., 1994), but the circumference at the base and the width were also measured in this study to get a better assessment of the possible effect of the attachment of the sternocleidomastoid muscle.

The height and breadth of the scapula were also observed displaying bilateral asymmetry (M. L. Osborn, unpublished data). Since the trapezius muscle attaches to the spine of the scapula, the length of the spine was chosen as an additional measurement.

The diameter and circumference of the clavicle were selected as measurements because of the attachment site of the sternocleidomastoid muscle. Most of the sternocleidomastoid muscle attachments sites were not rugose or robust, so they had to be estimated.

The diameter of the humerus was selected because bilateral asymmetry in humeri has been attributed to the preferential use of one side (Schulter-Ellis, 1980; Stirland, 1993; Sládek *et al.,* 2007). Since the head of the humerus is considered to be part of the shoulder girdle and would thereby be affected by shoulder moevement, the humerus should have measurable asymmetries caused by the muscles that attach on it: supraspinatus, infraspinatus, teres major and minor, pectoralis major, coracobrachialis, etc. (Pick and Howden, 1995).

The mandible was selected as a bone presumably not related to the hypothesized complex and would, thereby, show the asymmetry that was found in the body that would not be related to preferential hand, arm and shoulder use. The maximum height of the ascending ramus of the mandible was selected because it involved measuring both sides of the mandible. The condyle width was measured because bilateral asymmetry had been noticed in previous skeletal observations (M. L. Osborn, unpublished data).

The diameter of the first rib at the scalene tubercle was selected because of its close proximity to the clavicle, but not initially considered to be part of the hypothesized complex.

The circumference of the femur was selected as a feature presumably not related to the hypothesized complex because the legs are used evenly in everyday walking (Dusewicz and Kershner, 1969; Peters and Durding, 1979), even if some people show a preference for a particular side, such as always stepping first with the right leg. Therefore, asymmetry in the femur would be less than in the upper body.

2.2.3 Description of Measurements

2.2.3.1. Mastoid Process

Length: From the top of the external auditory meatus to mastoidale (i.e., the distal-most point of the mastoid process) at a 90 degree angle to the zygomatic arch as reported by Keen (1950:70; see also Giles and Elliot, 1963: 58-59; Moore-Jansen *et al*., 1994: 57).

Circumference: At the base of the mastoid process along the mastoid notch (i.e., digastric groove).

Width: From the posterior ridge of the external auditory meatus to the widest point of the mastoid process where it blends with the rest of the skull.

2.2.3.2. Scapula

Height: From the inferior border of the scapula to its superior border (Hrdlička, 1920: 130; Martin and Saller, 1959: 528; Montagu, 1960: 68; Olivier, 1969: 219; Moore-Jansen *et al*., 1994: 62; Bass, 1995: 122).

Breadth: From the midpoint on the border of the glenoid fossa to the midpoint on the end of the spine of the scapula (Hrdlička, 1920: 131; Martin and Saller, 1959: 528; Montagu, 1960: 68-70; Moore-Jansen *et al*., 1994: 62; Bass, 1995: 122).

Length of Spine: From the tip of the acromion to the midpoint on the medial border of the spine of the scapula (Bass, 1995: 122).

2.2.3.3. Clavicle

Diameter: At the level of the sternocleidomastoid muscle attachment site.

Circumference: At the level of the sternocleidomastoid muscle attachment site.

Length: From the medial end to the lateral end (Martin and Saller, 1959: 527; Olivier, 1969: 214; Moore-Jansen *et al*., 1994: 61; Bass, 1995: 131-132).

2.2.3.4. Humerus

Diameter: At mid-length (i.e., midshaft) (Moore-Jansen *et al*., 1994: 63-64).

2.2.3.5. Mandible

Height of Ascending Ramus: From gonion (i.e., the point at the angle of the mandible) to the superior-most point on the condyle (Moore-Jansen *et al*., 1994: 60; Bass, 1995: 84).

Condyle Width: Maximal (transverse) width of the condyle.

2.2.3.6. First Rib

Diameter: At the level of the scalene tubercle.

2.2.3.7. Femur

Circumference: At mid-length (i.e., midshaft).

2.2.4. Measurement Error

To ascertain measurement error, one specimen of each bone (i.e., cranium, clavicle, scapula, humerus, first rib, femur, and mandible) was selected from the Physical Anthropology Cadaver

Collection at Louisiana State University. Each character was measured ten times on the same bone. The standard deviation from these sets of measurements was used as the measurement error for each characteristic.

2.2.5. Morphological Characteristics

In addition to the measurements, one morphological difference was also recorded in a subsample of 11 individuals. On the back of the skull, the obvious "m" shape of the superior nuchal line was recorded, because bilateral asymmetry was observed in several individuals. One side of the "m" often rose higher and was straighter than the other side. The frequency of the superior nuchal line within the population was analyzed qualitatively. Since the superior nuchal line was a non-mensural character, it was not included in the postulated asymmetry patterns, but was compared to the width of the mastoid process and handedness.

2.3. Analysis of Bilateral Asymmetry

2.3.1. Ascertaining Significance of Asymmetry Based on Function

For each character pair, the difference between the right and left measurement was computed. This differential value was established by subtracting the right measurement from the left measurement. For individuals with greater right measurements, the differential value was negative; for individuals with greater left measurements, the differential value was positive. Therefore, each differential value represented the degree of asymmetry in each individual character pair. If the differential value for a character pair was less than or equal to the measurement error, it was not considered significantly asymmetrical and removed from further analysis.

In order to estimate the degree of asymmetry that reasonably could be assumed to be meaningful for each character pair, a threshold was established. Because Coren and Porac

(1977) reported that right-handed individuals comprise approximately 90% of a population and left-handed individuals comprise the remaining approximate 10%, and because an internet search produced numbers ranging from 70% to 90% for right-handed individuals and 10% to 30% for left-handed individuals (Holder, 2008), a conservative 85% of individuals displaying an asymmetrical character pair was used as the threshold for meaningful asymmetry of a particular character pair. Therefore, for each character, the percent of asymmetrical character pairs was established. If this percentage was above 85%, then the asymmetry was assumed to be due to function (i.e., preferential use) and not to chance.

The directions of asymmetry in these character pairs were then used to postulate left- and right-handed patterns (See results). Since the majority of the subsample was right-handed, the majority direction of asymmetry was assumed to be indicative of right-handedness, irrespective of whether the greater side of the character pair was on the right or the left. Conversely, the minority direction of asymmetry was assumed to be indicative of left-handedness. These postulated patterns were then compared to the patterns of individuals (see Results).

2.3.2. Analysis of Directional Asymmetries in Individuals of Known Handedness

The number of individuals displaying character pairs with asymmetry patterns in concordance with the postulated asymmetry patterns was tallied to show how well the individual asymmetry patterns were concordant with the postulated asymmetry patterns. The number of individual character pairs with asymmetry patterns in concordance with the postulated asymmetry pattern was also tallied.

2.3.3. Testing the Validity of the Postulated Asymmetry Patterns

The validity of the postulated asymmetry patterns was tested by comparing each individual's asymmetry pattern to either the right- or left-handed postulated asymmetry pattern. The individuals were grouped according to how many of their character pairs expressed asymmetries that were concordant with those in the postulated asymmetry pattern.

Twenty-nine right-handed individuals and three left-handed individuals were missing one or more character pairs and, therefore, were not included in the tests of validity of the postulated asymmetry patterns. The asymmetry patterns of their available character pairs were used in the analysis of directional asymmetries in individuals of known-handedness.

3. Results

3.1. Asymmetry Patterns of Characters

The standard deviation from the 14 character pairs was used as the measurement error for each characteristic (Table 1).

Table 1. Measurement error (standard deviation) for each character from the Physical Anthropology Teaching Collection at Louisiana State University. All measurements in mm.

Character	Mean ± SD
Length of mastoid	30.5 ± 1.1
Circumference at base of mastoid	53.1 ± 2.3
Width of mastoid	19.0 ± 0.4
Height of scapula	152.1 ± 0.5
Breadth of scapula	109.2 ± 0.3
Length of scapular spine	160.4 ± 10.4
Diameter of clavicle	15.4 ± 1.9
Circumference of clavicle	52.4 ± 5.9
Length of clavicle	155.0 ± 0.0
Diameter of humerus	26.3 ± 0.01
Width of mandibular condyle	20.8 ± 0.07
Height of mandibular ramus	53.4 ± 1.5
Diameter of first rib	4.2 ± 0.1
Circumference of femur	87.2 ± 0.7

Seven of these character pairs show at least 85% of individuals from the Bass collection showing asymmetry greater than the measurement error: width of the mastoid process, length of the clavicle, height of the scapula, breadth of the scapula, diameter of the humerus, width of the mandibular condyle, and diameter of the first rib. Of these seven characters, five of them were significantly different: width of the mastoid process, length of the clavicle, breadth of the scapula, diameter of the humerus, and diameter of the first rib (Table 2).

Table 2. Characters with ≥ 85% of individuals showing asymmetry greater than measurement error and paired t-test results (two-tailed). All measurements in mm.[1]

Character	Individuals	Left mean ± SD	Right mean ± SD	*P* (two-tailed)
Width of mastoid process	101	21.8 ± 3.6	22.7 ± 3.6	< 0.001
Length of clavicle	87	158.3 ± 8.3	157.0 ± 9.5	0.033
Height of scapula	94	159.6 ± 14.3	159.8 ± 14.4	0.712
Breadth of scapula	95	106.7 ± 16.3	105.9 ± 16.2	< 0.001
Diameter of humerus	98	23.7 ± 1.9	24.3 ± 2.1	< 0.001
Width of mandibular condyle	100	20.2 ± 3.7	20.0 ± 3.8	0.297
Diameter of first rib	89	3.9 ± 0.9	4.1 ± 1.1	0.01

[1]Character pairs that are significantly asymmetrical are highlighted. Statistical significance is set as $P < .05$.

In the sample of 101 individuals, a subsample of 62 individuals was of known handedness, with 54 individuals (87%) being right-handed and eight individuals (13%) being left-handed. This coincides with the proportions of 85% versus 15% that were used to select the meaningfully asymmetrical character pairs based on function (see above). The means of the five characters were then compared for these individuals of known handedness. Although only three character pairs displayed significant asymmetry in the subsample of individuals of known handedness, the means display the same direction of asymmetry as the entire sample (Table 3). The direction of asymmetry for the means of each character pair for left- or right-handedness was then assembled and used to postulate asymmetry patterns for left- and right-handed individuals. These postulated patterns comprised the character pairs that were significantly different (Table 2) in this order: (1) width of the mastoid process; (2) length of the clavicle; (3) breadth of the scapula; (4) diameter of the humerus; and (5) diameter of the first rib.

Table 3. Paired t-test results (two-tailed) for subsample of individuals of known handedness. All measurements in mm.[1]

Character	Individuals	Left mean ± SD	Right mean ± SD	*P* (two-tailed)
Width of mastoid process	53	21.1 ± 3.6	22.7 ± 3.6	< 0.001
Length of clavicle	55	156.9 ± 8.2	156.2 ± 9.7	0.354
Breadth of scapula	54	108.9 ± 5.4	108.0 ± 6.0	< 0.001
Diameter of humerus	59	23.7 ± 1.8	24.6 ± 2.0	< 0.001
Diameter of first rib	48	3.9 ± 1.0	4.1 ± 0.9	0.064

[1]Character pairs that are significantly asymmetrical are highlighted. Statistical significance is set as $P < .05$.

For each individual, the direction of asymmetry for each character pair was represented by an "R" or an "L". For example, an "R" represents that the mean for that character pair was directionally asymmetrical toward the right side. An "L" represents that the mean for that character pair was directionally asymmetrical on the left side. Therefore, the right-handed postulated asymmetry pattern is represented as RLLRR and the left-handed postulated asymmetry pattern is represented as LRRLL.

3.2. Overview of Individual Variability in Asymmetry

Twenty-nine right-handed individuals and three left-handed individuals were either missing measurements for character pairs or had one or more differential values from characters pairs that were below the measurement error (Tables 4 and 5). These individuals did not display complete asymmetry patterns and, therefore, their individual asymmetry patterns were not compared to the postulated asymmetry patterns.

Table 4. Asymmetry patterns of right-handed individuals with incomplete sets of character pairs in comparison with the right-handed postulated asymmetry pattern.[1]

Number of concordance	Number of individuals	ID number	Width of mastoid R	Length of clavicle L	Breadth of scapula L	Diameter of humerus R	Diameter of first rib R
4	2	42, 69					
	1	92					
	2	48, 59					
	1	67					
3	2	32, 62					
	2	28, 33					
	1	10					
	1	34					
	1	38					
	1	60					
	1	61					
	1	78					
	1	86					
2	1	18					
	1	35					
	1	66					
	1	76					
	1	87					
	1	97					
1	1	3					
	1	37					
	1	54					
	1	75					
	1	82					
	1	89					

[1]Dark grey squares represent character pairs that are in concordance with the right-handed postulated asymmetry pattern. White squares represent character pairs that are not in concordance with the right-handed postulated pattern. Vertically-striped squares represent character pairs that are missing. Diagonally-striped squares represent character pairs in which the differential value was below the measurement error.

Table 5. Asymmetry patterns of left-handed individuals with incomplete sets of character pairs in comparison with the left-handed postulated asymmetry pattern.[1]

Number of concordance	Number of individuals	ID number	Width of mastoid L	Length of clavicle R	Breadth of scapula R	Diameter of humerus L	Diameter of first rib L
2	1	13					
	1	93					
	1	100					

[1]Dark grey squares represent character pairs that are in concordance with the left-handed postulated asymmetry pattern. White squares represent character pairs that are not in concordance with the left-handed postulated pattern. Vertically-striped squares represent character pairs that are missing. Diagonally-striped squares represent character pairs in which the differential value was below the measurement error.

Among individuals who were known to be right-handed, 71% (32 of 45) show asymmetry in the mastoid process concordant with the postulated pattern for right-handed individuals (Fig. 1). The corresponding percentages for the other characters are 60% (28 of 47) for the clavicle, 72% (34 of 47) for the scapula, 92% (47 of 51) for the humerus, and 57% (24 of 42) for the first rib.

Among individuals who were known to be left-handed, 50% (four of eight) show asymmetry in the mastoid process concordant with the postulated pattern for right-handed individuals (Fig. 1). The corresponding percentages for the other characters are 63% (five of eight) for the clavicle, 43% (three of seven) for the scapula, 63% (five of eight) for the humerus, and 50% (four of eight) for the first rib.

The asymmetry patterns of the character pairs of the right-handed individuals (Fig. 2) are variably concordant with one to five character pairs of the postulated asymmetry pattern. Among individuals who were known to be right-handed, 76% (20 of 25) display asymmetry patterns with two, three or four of the character pairs being concordant with the right-handed postulated asymmetry pattern. Only 20% (five of 25) of these individuals display asymmetry patterns with five character pairs being completely concordant with the right-handed asymmetry pattern.

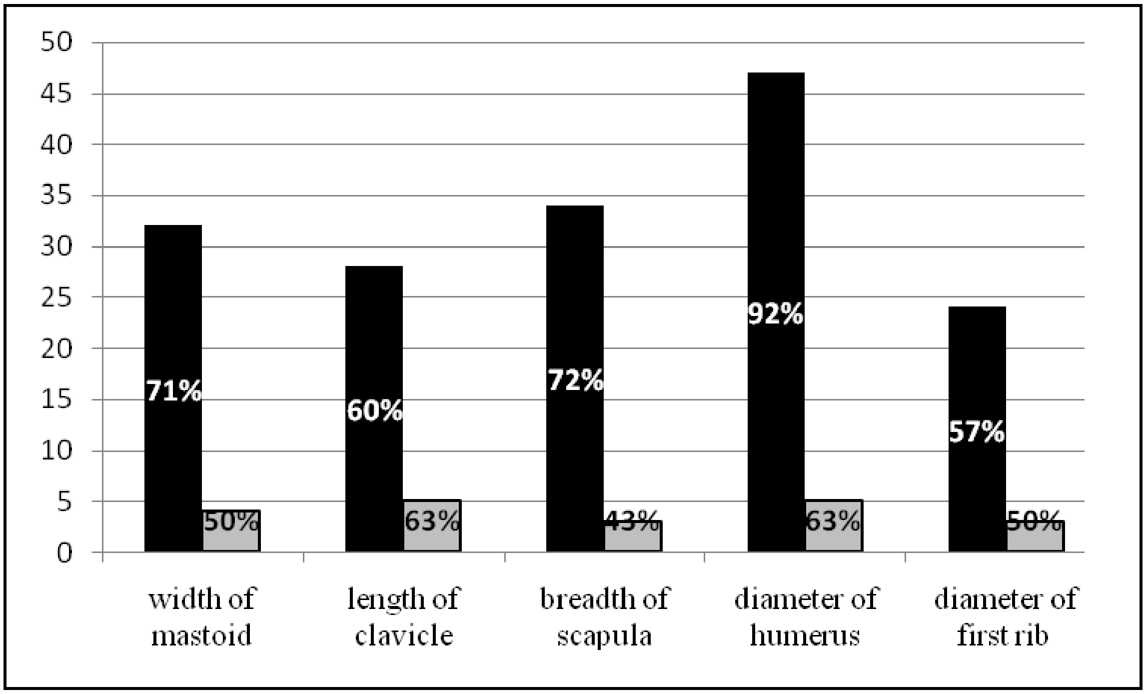

Figure 1. Number and percentage of character pairs from right-handed individuals (taller, left columns, black) and left-handed individuals (lower, right columns, grey) whose asymmetry is concordant with the asymmetry of particular character pairs established in the right- and left-handed postulated asymmetry patterns, respectively.

The asymmetry patterns of the character pairs of left-handed individuals (Fig. 2) are variably concordant with two or three character pairs of the postulated asymmetry pattern. Among individuals who were known to be left-handed, 40% (two of five) display asymmetry patterns with two character pairs being concordant with the left-handed asymmetry pattern. The remaining 60% (three of five) display asymmetry patterns with three character pairs being concordant with the left-handed asymmetry pattern.

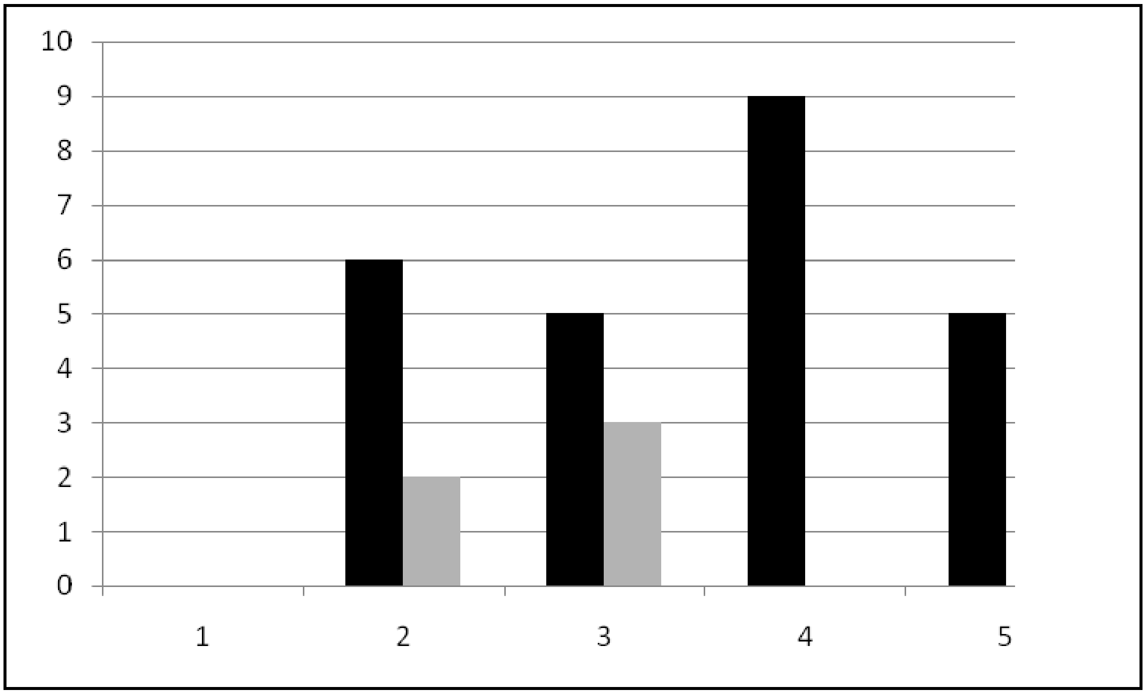

Figure 2. Number of right-handed individuals (taller, left columns, black) and left-handed individuals (lower, right columns, grey) displaying asymmetry patterns with a particular number (1-5) of character pairs being concordant with the right- or left-handed postulated asymmetry patterns, respectively.

3.3. Asymmetry Patterns in Right-handed Individuals

Concordance of all five asymmetrical character pairs (i.e., width of the mastoid process, length of the clavicle, breadth of the scapula, diameter of the humerus, and diameter of the first rib) with the postulated asymmetry pattern of five character pairs is displayed by only five (i.e., ID numbers 8, 46, 70, 74, and 84) out of the 25 right-handed individuals (Fig. 2 and Table 6).

Among the right-handed individuals showing concordance with four, three, and two characters with that of the postulated pattern, there is a variation among individuals in which characters are concordant. For example, among the individuals with four concordant character pairs, four individuals show discordance with the diameter of the first rib, two show discordance with length of the clavicle, two show discordance with breadth of the scapula, and one shows discordance with diameter of the humerus (Table 6).

Table 6. Asymmetry patterns of right-handed individuals in comparison with the right-handed postulated asymmetry pattern.[1]

Number of concordance	Number of individuals	ID number	Width of mastoid **R**	Length of clavicle **L**	Breadth of scapula **L**	Diameter of humerus **R**	Diameter of first rib **R**
5	5	8, 46, 70, 74, 84	■	■	■	■	■
4	4	4, 30, 43, 72	■	■	■	■	
	2	20, 36	■		■	■	■
	2	29, 64	■	■		■	■
	1	91	■	■	■		■
3	2	2, 51	■	■		■	
	1	49	■		■	■	
	1	79	■			■	■
	1	88			■	■	■
2	3	31, 57, 65			■	■	
	1	44	■		■		
	1	19	■			■	
	1	39			■		■

[1]Dark grey squares represent character pairs that are in concordance with the right-handed postulated asymmetry pattern. White squares represent character pairs that are not in concordance with the right-handed postulated pattern.

3.4. Asymmetry Patterns in Left-handed Individuals

The sample size of left-handed individuals is too small for meaningful results. Still, the available data are intriguing. None of the left-handed individuals display concordance of all five or even four significantly asymmetrical character pairs (i.e., width of the mastoid process, length of the clavicle, breadth of the scapula, diameter of the humerus, and diameter of the first rib) with the postulated asymmetry pattern of five character pairs (Fig. 2 and Table 7).

Table 7. Asymmetry patterns of left-handed individuals in comparison with the left-handed postulated asymmetry pattern.[1]

Number of concordance	Number of individuals	ID number	Width of mastoid **L**	Length of clavicle **R**	Breadth of scapula **R**	Diameter of humerus **L**	Diameter of first rib **L**
3	1	7					
	1	5					
	1	68					
2	1	63					
	1	58					

[1]Dark grey squares represent character pairs that are in concordance with the left-handed postulated asymmetry pattern. White squares represent character pairs that are not in concordance with the left-handed postulated pattern.

Among the left-handed individuals showing concordance with three and two characters with that of the postulated pattern, there is a variation among individuals in which characters are concordant. For example, among the individuals with three concordant character pairs, one individual shows discordance with diameter of the humerus and diameter of the first rib, one shows discordance with breadth of the scapula and diameter of the humerus, and one shows discordance with width of the mastoid and breadth of the scapula (Table 7).

3.5. Asymmetry Patterns Involving the Superior Nuchal Line, Mastoid Process, and Handedness

The rise of the superior nuchal line was the one non-mensural character in this study and, therefore, could not be included in the postulated asymmetry pattern. Still, the rise of the superior nuchal line shows directional asymmetry (Fig. 3A) in right-handed individuals, which parallels the directional asymmetry of the width of the mastoid process. The sample size of the rise of the superior nuchal line in left-handed individuals (Fig. 3B) is too small for meaningful results.

The asymmetry pattern observed in the rise of the superior nuchal line was compared in nine right-handed individuals to the asymmetry pattern observed in the width of the mastoid process and their handedness (Fig. 3A). In eight of the nine right-handed individuals (i.e., ID numbers 8, 9, 28, 43, 49, 60, 69, and 86), the asymmetry pattern of the superior nuchal line matches the asymmetry pattern of the width of the mastoid process and their handedness. In one of the nine right-handed individuals (i.e., ID number 34), the asymmetry of the superior nuchal line matches the width of the asymmetry of the mastoid, but not his handedness.

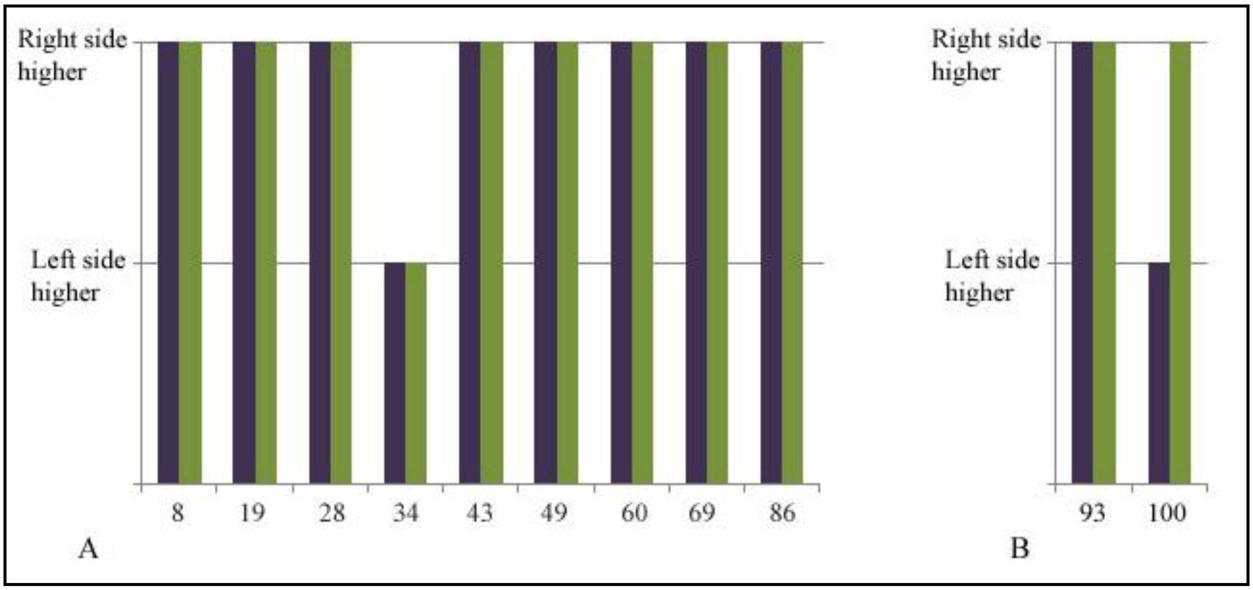

Figure 3. Asymmetry patterns of the width of the mastoid process (left column, dark blue) and the rise of the superior nuchal line (right column, green) for right-handed individuals (A) and left-handed individuals (B). Identified by ID numbers.

4. Discussion

4.1. Significance of Asymmetries

The preferential use of one side over the other will be evidenced on the involved skeletal structures (Trinkaus *et al.*, 1994; Kannus *et al.*, 1995; Steele and Mays, 2005; Ruff *et al.*, 2006). This is known as bilateral asymmetry. When the majority of individuals in a human population preferentially use the right hand and arm, they display directional asymmetry (Van Valen, 1962; Coren and Porac, 1977; Holden, 2008) and, thus, they show non-random morphological asymmetry toward the right side.

Although all of the character pairs in this study were selected based on functional considerations to test a working hypothesis, seven out of 14 character pairs displayed a degree of asymmetry that was not above the measurement error. However, five of the character pairs displayed asymmetry that was above the measurement error and also significantly directional. A sixth, non-mensural character pair also displayed directional asymmetry. These six character pairs predicted right-handedness to varying degrees. Four of the characters had 70% or more of right-handed individuals displaying asymmetry toward the same side: rise of the superior nuchal line, breadth of the scapula, diameter of the humerus, and width of the mastoid. Two of the asymmetrical character pairs displayed weaker directional asymmetry, with more than 50% but less than 70% of right-handed individuals displaying asymmetry towards the same side: length of the clavicle and diameter of the first rib. However, the asymmetries observed in these six character pairs can be explained in causal terms.

4.2. Significance of Asymmetry in the Superior Nuchal Line and Scapula

Among the character pairs showing directional asymmetry, the comparably high degree of asymmetry of the rise of the superior nuchal line, width of the mastoid process and the breadth of the scapula indicate that a functional relationship may exist. This hypothesis is supported by the trapezius muscle, which attaches on the medial third of the superior nuchal line of the skull and along the spine of the scapula (Pick and Howden, 1995). The trapezius muscle, however, is a complex muscle with at least three portions and several different attachments and, for this reason, may affect the morphology of several characters but to varying degrees.

Generally, the trapezius muscle suspends, elevates, and supports the scapula, especially when a load is carried in a hand or applied directly to the shoulder (Basmajian, 1980; Pick and Howden, 1995). More specifically, according to Basmajian (1979), Cartmill *et. al.* (1987), Biel (2001), and Moore and Dalley (2006), the upper portion of each trapezius muscle elevates the scapula. The left and right upper trapezius muscles extend the head and neck when contracting together, but when contracting individually, they flex the head and neck to the left or right side, respectively, or rotate the head and neck to the opposite side (Biel, 2001). They also elevate the scapula and rotate it superiorly. When contracting together, the left and right middle portions of the trapezius muscles fix the scapula in place (Basmajian, 1979; Biel, 2001). When contracting individually, the left and right middle trapezius muscles each adduct a scapula (Basmajian, 1979; Biel, 2001; Moore and Dalley, 2006). The lower portions of the trapezius muscles depress each scapula (Basmajian, 1979; Cartmill *et. al*. 1987; and Biel, 2001). The lower trapezius muscles also act with the upper trapezius muscles in rotating the scapula (Moore and Dalley, 2006).

4.3. Significance of Asymmetry in the Humerus

The directional asymmetry of the diameter of the humerus at the midshaft indicates that it is causally related to the cranio-cervico-omo-clavicular complex, because it lies just beneath the attachment site of the deltoid muscle (i.e., deltoid tuberosity). The deltoid muscle also attaches to the clavicle and the scapula, so that it pulls on the humerus and abducts it during the lifting of objects (Pick and Howden, 1995). Since one side is often used preferentially during this activity, asymmetry in this character can be expected.

Because a load on the arm exerts tension on the humerus, which is pulled toward the shoulder joint by the deltoid muscle, one would expect that the length of the humerus would also show directional asymmetry. Indeed, this prediction is confirmed by the observations of Schulter-Ellis (1980) and Steele and Mays (2005). This idea, however, occurred after the original data had been analyzed and interpreted, so the asymmetry of the length of the humerus in this sample remains to be assessed.

4.4. Significance of Asymmetry in the Mastoid Process

The directional asymmetry of the width of the mastoid process points to some underlying mechanical causes, in particular because it serves as attachment site for at least part of the sternocleidomastoid muscle. The sternocleidomastoid muscle, like the trapezius muscle, is a complex muscle. It consists of a sternal portion and a clavicular portion. The sternal portion attaches to the sternum and the mastoid process. The clavicular portion attaches to the clavicle and partly to the mastoid process, extending backwards onto the occipital region of the skull at the level of the superior nuchal line (Pick and Howden, 1995). According to Simons *et al*. (1999) and Biel (2001), the left and right sternocleidomastoid muscles bend the head forward when contracting at the same time, but when they contract separately, they flex the head and neck to the left or right side, respectively, or rotate them to the opposite side. The sternocleidomastoid muscle, however, acts with the trapezius muscle. According to Simons *et al.* (1999), the sternocleidomastoid muscle counteracts and “checkreins” the trapezius muscle when the head and neck are tilted back, so that the head is stabilized and does not fall backwards.

The sternocleidomastoid and trapezius muscles not only perform closely coordinated actions, but also are innervated by the accessory nerve (i.e., cranial nerve XI), develop from the same embryonic primordium, and are located in the same fascial pocket (Cartmill *et al.*, 1987). These two muscles also run along the same level of the skull: the attachment of the sternocleidomastoid muscle runs along the mastoid process onto the skull and toward the attachment of the trapezius muscle (Pick and Howden, 1995).

The trapezius muscle pulls on the back of the skull at the superior nuchal line during every motion of the shoulder, and the sternocleidomastoid muscle acts as a guy rope that is anchored to the clavicle to stabilize the head during shoulder movements. For example, when an individual carries a load in each hand, the weight of the loads exerts a downward pull on the shoulders, but the trapezius muscles pull the shoulders upward at the same time so that the shoulders are held in place. Normally, the head does not extend at this time, even though the trapezius muscle exerts a backward pull on it, because the sternocleidomastoid muscles are counteracting this pull by a forward force, thereby holding the head in place. When an individual carries a load only in one hand, however, the one-sided load must be counterbalanced by bending the body toward the opposite side to maintain overall balance. In healthy individuals, this is achieved by the core vertebral muscles that move and stabilize the vertebral column. Then the sternocleidomastoid and trapezius muscles are free to move the shoulder girdle independently from and relative to the vertebral column (personal communication with D. G. Homberger; see also Moore and Dalley, 2006). This scenario is supported by the results that only the width of the mastoid process is directionally asymmetrical, but not its length in this study. If the sternal portion of the sternocleidomastoid muscle is not influenced by shoulder movements while stabilizing the head, the length of the mastoid process would be less likely to be asymmetrical. The clavicular portion, in contrast, is influenced by shoulder movements. Therefore, asymmetry in its attachment sites on the mastoid process and superior nuchal line would be expected. While this is observed in the directional asymmetry of the width of the mastoid process, this is not the case for the attachment on the clavicle where the diameter was measured. This lack of quantifiable asymmetry in this character may be an artifact of the measuring method which required estimation of the attachment site because its rugosity was often barely noticeable.

4.5. Significance of Asymmetry in the Clavicle

The left clavicle of humans is usually longer than the right one (Parsons, 1916; Schultz, 1937; Huggare and Houghton, 1995; Mays *et al*., 1999; Andermahr *et al.*, 2007). The current study confirms this observation, but the percentage of directional asymmetry in this character pair is less than in the humerus. One could be tempted to tie the observation that the majority of people have a longer left clavicle to the fact that the majority of individuals are right-handed. However, the degree of asymmetry in the length of the clavicle only matched the asymmetry pattern of this character in the postulated right-handed asymmetry pattern (i.e., the left clavicle being longer in right-handed individuals) in a little over half (58%) of the right-handed individuals in the current study . Hence, asymmetry in this character pair is not a strong or reliable predictor of handedness.

The weak directional asymmetry observed in the length of the clavicle in right-handed people can be explained within the context of the biomechanics of the cranio-cervico-omo-clavicular complex. Because the fibers of the trapezius muscle are oriented obliquely from the shoulder to the superior nuchal line of the head, when the trapezius muscle is contracting, it generates a force that elevates the scapula and also tends to compress the clavicle (see Mays *et al*., 1999). In these conditions, the clavicle acts like a spoke in a wheel. However, while the trapezius muscle contracts for virtually all shoulder movements, the clavicle is not necessarily under compression during all of them. For example, the clavicle is not compressed when the shoulder is retracted or abducted. Therefore, the length of the clavicle would be expected to be less strongly asymmetrical in right-handed individuals than the rest of the significantly asymmetrical character pairs in this study.

The diameter of the clavicle at the sternocleidomastoid attachment site, where the clavicular portion of the muscle attaches, was also measured and found not to be asymmetric. The reasons for this lack of asymmetry are discussed in section 4.4.

4.6. Significance of Asymmetry in the First Rib

The diameter of the first rib was originally selected as a measurement that was expected, for functional reasons, to be essentially symmetrical and, therefore, could be used as a standard against which to measure the degree of asymmetry in other measurements that were expected to be asymmetrical. Contrary to this expectation, however, the diameter of the fist rib turned out to be significantly asymmetrical. This asymmetry is most likely related to the function of the scalene muscle that attaches on the first rib where the diameter was measured.

The scalene muscle, like the trapezius and sternocleidomastoid muscles, is a complex muscle. It has three portions that attach to the cervical vertebrae and the first two ribs, but only the portion attaching to the first rib will be discussed further (Pick and Howden, 1995). The weak directional asymmetry observed in the diameter of the first rib in right-handed people can be explained within the context of the biomechanics of the cranio-cervico-omo-clavicular complex. This portion (i.e., the anterior scalene) attaches to the 3rd, 4th, 5th, and 6th cervical vertebrae and to the scalene tubercle on the first rib. As described above (see section 4.4), the anterior scalene is one of the core vertebral muscles that moves and stabilizes the vertebral column when the head and neck are bent to one side in order to counteract the force produced by a load carried in only one hand (personal communication with D. G. Homberger; see also Moore and Dalley. 2006). As with the clavicle, the anterior scalene muscle is not necessarily activated in every shoulder movement. Therefore, the diameter of the first rib would be expected to be less strongly asymmetrical in right-handed individuals than the rest of the significantly asymmetrical character pairs in this study.

4.7. Patterns of Asymmetry and the Cranio-cervico-omo-clavicular Complex

Each character that is part of a significantly asymmetrical character pair in this study (i.e., rise of the superior nuchal line, breadth of the scapula, diameter of the humerus, width of the mastoid process, length of the clavicle, and diameter of the first rib) displayed directional asymmetry and was shown to be connected through the actions of the trapezius, sternocleidomastoid and scalene muscles during movements of the shoulder and arm, at least in right-handed individuals. This observation provides support for the existence of the postulated cranio-cervico-omo-clavicular complex.

The data for right-handed individuals show that six characters were directionally asymmetrical. The data for left-handed individuals, however, were not informative with respect to directional asymmetry for several reasons. First, the subsample of left-handed individuals was small, with only eight individuals. This sample is too small to be meaningful. Future studies of a larger sample may reveal whether the lack of concordance between the character pairs in left-handed individuals and the postulated asymmetry pattern in this study is due to the small sample size or to the fact that left-handed individuals generally have to conform to an environment that is built for right-handed people (Holder, 2008).

The observation (at least for the right-handed individuals of this study) that some character pairs varied in the concordance of their asymmetry pattern with the postulated asymmetry pattern may be explained by the variability of the frequency and intensity of physical exercise among individuals, especially in the increasingly sedentary people of the U. S. A. Many individuals likely have a limited range and frequency of movement and may, therefore, exhibit little directional asymmetry in their character pairs.

The working hypothesis for this study suggested that the unique shape and size of the mastoid process and clavicle in humans developed and evolved in response to the development and evolution of erect posture and bipedality, in the course of which the shoulder girdle essentially became suspended from the skull. This suspension of the shoulder girdle allows the arms to move independently from the rest of the body. The conjecture that the mastoid process and clavicle, as well as several other structures, are related by function within the cranio-cervico-omo-clavicular complex is supported by some of the results from this study. Many of the original characters that were measured were not significantly different or did not exceed the measurement error and, therefore, were not used for further analysis. This does not mean that these characters are not involved with the cranio-cervico-omo-clavicular complex. Their exact relationship within the complex is not yet known. Future tests of this hypothetical complex will be geared toward a more complete understanding of the manner in which all relevant structures are functionally related.

The results from this current research show that, in right-handed individuals, there is evidence of a functional relationship between the head and shoulders. This functional relationship is evidenced in the asymmetries in the width of the mastoid process, rise of the superior nuchal line, diameter of the humerus, and breadth of the scapula.

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Vita

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